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Species roles in plant-pollinator communities are conserved across native and alien ranges

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ABSTRACT

Aim. Alien species alter interaction networks by disrupting existing interactions, for example between plants and pollinators, and by engaging in new interactions. Predicting the effects of an incoming invader can be difficult, although recent work suggests species roles in interaction networks may be conserved across locations. We test whether species roles in plant-pollinator networks differ between their native and alien ranges, and whether the former can be used to predict the latter.

Location: worldwide.

Methods. We used 64 plant-pollinator networks to search for species occurring in at least one network in its native range and one network in its alien range. We found 17 species meeting these criteria, distributed in 48 plant-pollinator networks. We characterized each species' role by estimating species-level network indices: normalised degree, closeness centrality, betweenness centrality, and two measures of contribution to modularity (*c* and *z* scores). Linear Mixed Models and Linear Regression Models were used to test for differences in species role between native and alien ranges and to predict those roles from the native to the alien range, respectively.

Results. Species roles varied considerably across species. Nevertheless, although species lost their native mutualists and gained novel interactions in the alien community, their role did not differ significantly between ranges. Consequently, closeness centrality and normalised degree in the alien range were highly predictable from the native range networks.

Main conclusions. Species with high degree and centrality define the core of nested networks. Our results suggest that core species are likely to establish interactions and be core

species in the alien range, whilst species with few interactions in their native range will behave similarly in their alien range. Our results provide new insights into species role conservatism, and could help ecologists to predict alien species impact at the community level.

Key-words: biological invasions, centrality, conservatism, ecological networks, pollination, predicting invasion

INTRODUCTION

Predicting novel species interactions is a crucial challenge in today's rapidly changing world. Alien species are an important driver of novel ecosystems (Hobbs *et al.*, 2006) due to their ability to outcompete native species (Chittka & Schurkens, 2001; Madjidian *et al.*, 2008; Roy *et al.*, 2012), change the community structure (Albrecht & Gotelli, 2001; Memmott & Waser, 2002; Carpintero *et al.*, 2005) and disrupt species interactions (Aizen et *al*., 2008; Traveset & Richardson, 2006; Tylianakis *et al.*, 2008). Studies on alien species mostly focus on species considered to be invasive, which means that rather little is known about those alien species that remain at low population size or have fewer interactions with (and hence, impact on) the recipient community.

While many studies have tried to identify key features that predict which species will become invasive and which communities are more likely to be invaded (Thuiller *et al.*, 2005; Richardson & Pysek, 2006; Pysek & Richardson, 2007) these remain of limited practical value. For example it remains difficult to predict whether a mutualistic interaction will facilitate the establishment and dispersal of an alien species (Hulme, 2012). The limited practical value of current work is partially due to the need for detailed information on each species involved in the potential novel interactions, which is usually very time consuming to gather. Therefore, new methods to simplify predictions are required. An alternative could be to assess the role a given species plays in the topology of interaction networks (e.g. Stouffer et al. 2012; Martin Gonzalez *et al.*, 2010; Albrecht et al. 2014). Species roles summarize their ability to interact with, and potentially affect, other species in the community in a way that is relatively easy to sample compared with measures of multiple species and community traits. The application of species roles in ecological networks to predict invasion currently remains untested.

71 Ecological networks have been of considerable use when trying to understand how
72 alien species integrate into local communities (Memmott & Waser, 2002; Garcia *et al.*, 2014,
73 Maruyama *et al*., 2016) and how they affect the overall mutualistic network structure (Olesen
74 *et al.*, 2002a; Santos *et al.*, 2012; Albrecht *et al.*, 2014). In general, alien species are
75 generalists, i.e. they interact with many species in the community in which they occur (Aizen
76 *et al.*, 2008; Santos *et al.*, 2012). Generalist species tend to occupy central positions in
77 ecological networks, and by interacting with other generalists and specialists (Memmott &
78 Waser, 2002; Aizen *et al.*, 2008) they contribute to the pattern of nestedness that
79 characterises many mutualistic networks (Bascompte, 2003; Bascompte & Jordano, 2007). In
80 addition to its number of direct interaction partners (termed 'degree'), a species' position
81 allows it to connect different parts of the network and maintain network cohesiveness. This
82 helps to define its role in structuring the overall network topology (Martin Gonzalez *et al.*,
83 2010), including elements of network structure such as clustering or modularity (Olesen *et*
84 *al.*, 2007). Thus, the species' position in the network, i.e. its network role, captures key
85 information on its interactions with, and potential effects on, other species in the community.

86 Recent work suggests that species roles are conserved across different locations.
87 Species interactions, either generalist or specialist, have been shown to be phylogenetically
88 conserved across space and time (Jordano *et al.*, 2003; Rezende *et al.*, 2007; Gómez *et al.*,
89 2010), because intrinsic (inherited) characteristics of species can constrain who can interact
90 with whom (Eklöf *et al.*, 2013) and can be related to native and alien species roles in network
91 topology (Maruyama *et al*., 2016). If these traits show low intraspecific variability across
92 locations, this indicates that species roles in networks should also be conserved. For example,
93 species roles in predator-prey networks can be conserved from an evolutionary perspective,

such that dynamically-important species in one network will be important in the other networks in which it occurs (Stouffer *et al.*, 2012). Similarly, species roles in host-parasitoid networks were found to be intrinsic characteristics conserved over different temporal and spatial scales (Baker *et al.*, 2015).

Despite evidence of an intrinsic component of species network roles, species interactions and network roles may also be affected by local environmental and biotic conditions (Tylianakis *et al.*, 2008; Trøjelsgaard *et al.*, 2015). Moreover, the number and type of interactions a species has increase with that species' abundance (e.g., Trøjelsgaard *et al*., 2015), and species abundance and interactions may change during different stages of invasion (Aizen *et al.*, 2008). Finally, patterns of non-random association among species based on their phylogenetic relatedness (Rezende *et al.*, 2007) suggest that coevolved interactions may be important for structuring mutualistic networks. Therefore, it is currently not clear whether species roles can be extrapolated from one location to another that differs in its evolutionary history and local community traits.

Here we aim to understand whether species roles differ and can be predicted from the native to the alien range of their distribution. Specifically, we use measures of plant and insect species roles in plant-pollinator networks (normalised degree, closeness and betweenness centrality, and *c* and *z* scores) recorded in both their native and alien ranges to test whether they differ consistently or can be predicted between ranges. Based on the findings that species roles and ecological interactions can be temporally, spatially and phylogenetically conserved (Rezende *et al.*, 2007; Gómez *et al.*, 2010; Stouffer *et al.*, 2012; Baker *et al.*, 2015) we predict that a species' network role will be similar in its native and alien

ranges, such that the former can be used to predict the latter. By including both specialist and generalist species we can draw conclusions about both rare and common alien species.

METHODS

We searched for plant-pollinator networks where we could potentially find species recorded in both their native and alien range. We found 48 plant-pollinator networks of which 42 were downloaded from the "Web of Life" database (Ortega, 2014), three are our own data sampled in New Zealand and three are unpublished data from Lopezaraiza-Mikel and Memmott in Hawaii; Table S1). Our criteria of species/network inclusion in the dataset was to have a target species occurring in at least one network as native and one network as alien. Thus each network can contain more than one target species, each of which may be either in its native or its alien range. As some of these networks contain only the presence/absence of interactions and the sampling effort of these networks is mostly unknown, we analysed all networks as binary matrices. In addition, here a flower visitor was considered to be a pollinator, irrespective of whether effective pollination was demonstrated. To define species range as native or alien, we used the following online information: Global Invasive Species Database (http://www.issg.org/database/welcome/), Global Invasive Species Information Network (http://www.gisin.org), Delivering Alien Invasive Species Inventories for Europe (http://www.europe-aliens.org/), GB Non-Native Species Secretariat Website (http://www.nonnativespecies.org), Plant Pest Information Network of New Zealand (http://archive.mpi.govt.nz/applications/ppin), Centre for Invasive Species and Ecosystem

Health (http://www.bugwood.org/), Weeds in Australia (http://www.environment.gov.au/biodiversity/invasive/weeds/), and Invasive Species of Japan (https://www.nies.go.jp).

Species roles

Species roles in networks can be described by a variety of different, yet often correlated metrics. Our intent here was not to provide an exhaustive comparison of different potential measures of species roles, or to determine which metrics were best conserved and why. Rather, we focused on testing a 'proof of concept' that roles could be conserved, so we focused on five complementary metrics that could potentially capture different aspects of species ecology:

1) Normalised degree – the number of interactions per species (i.e. degree) divided by the number of possible interacting partners, which controls for differences in network size. Normalised degree is the most local centrality index that characterizes a species' network position, such that species with high degree are core in the network structure and enhance robustness (Solé & Montoya, 2001; Dunne *et al.*, 2002). Additionally, normalised degree estimates how generalist/specialist a species is relative to other species in the same trophic level of the community in which it occurs.

2) Closeness centrality (hereafter, closeness) – the average distance (path length) to all other species in the network. Closeness incorporates the number of immediate connections to adjacent nodes and the connections of those nodes, so is a more global measure of location than degree. In bipartite networks, closeness and betweenness are

160 measured for the unipartite projection of each trophic level based on shared interaction
161 partners, such that higher closeness indicates a greater number of interaction partners shared
162 with other species in the same trophic level that also share partners with many other species
163 (Freeman, 1979; Martín Gonzalez *et al.*, 2010). Thus, closeness is a measure of niche overlap
164 with other species at the same trophic level via shared pollinators and the potential for either
165 positive or negative indirect effects via short path lengths (Morales & Traveset, 2008;
166 Carvalheiro *et al.*, 2014).

167 3) Betweenness centrality (hereafter, betweenness) – the proportion of the shortest
168 paths linking any pair of species in the network that cross through a given species. It estimates
169 species importance for network cohesiveness (Freeman, 1979; Martín Gonzalez *et al.*, 2010).
170 Species with high betweenness can potentially connect different parts of the network that
171 could be otherwise sparsely linked or even isolated; thus alien species that tend to be highly
172 generalist may be linking previously isolated species in plant-pollinator networks and affect
173 the overall network structure.

174 4) and 5) *c* and *z* scores: the combination of these two metrics describes a species'
175 role in the topology of the network as a hub, peripheral or connector within and among
176 modules (Olesen *et al.*, 2007) based on the modularity of the network (Guimera & Amaral,
177 2005). The *z*–score calculates the standardized number of links a species has within a module,
178 and the *c*–score calculates the among module connectivity, which is the number of links a
179 given species establishes among different modules. Therefore, high values of *c* and *z* are
180 related to generalist species that have many interactions throughout the whole network,
181 either as hubs connecting species within modules, or as connectors linking different modules.
182 On the other hand, low values of *c* and *z* describe peripheral species that tend to be specialists.

Alien plant species that invade a new range may act as network hubs by attracting many different pollinator species through providing high amounts of nectar, for example, Himalayan balsam (*Impatiens glandulifera* Royle) acts as a "magnet species" in its alien range (Chittka & Schurkens, 2001, Lopezaraiza-Mikel et al. 2007), whilst alien pollinator species may act as network connectors while searching for floral resources in different modules.

To allow comparisons across networks with different size, closeness and betweenness were each scaled to sum to 1. Species role metrics were calculated using bipartite (Dormann *et al.*, 2009) and rnetcarto packages (Doulcier, 2015) for R; correlations among these metrics are shown in Table S5.

Statistical analysis

Are there differences in species roles in their native vs. alien range?

To answer whether species roles differed from native to alien ranges we used Linear Mixed-Effects Models (LMMs) in the lme4 package (Bates *et al.*, 2014). Individual models were fitted for normalised degree, closeness, betweenness, and *c*- and *z*-scores. The first four metrics were logit transformed to solve the issue of being bounded from zero to one (Warton & Hui, 2011). Range (native vs. alien) was modelled as a fixed factor, whilst network and species were fitted as random effects to account for multiple observations from the same network and to group native and alien measures from the same species. Residual plots were used to check model adherence to assumptions. The overall variance explained by the model, and the proportion that could be attributed to the fixed factor (range) and the random factors were estimated by calculating: i) conditional Pseudo R-squared ($R^2GLMM_{(fix+rand)}$), to estimate total

variance explained by the fixed and random effects combined, ii) marginal Pseudo R-squared ($R^2GLMM_{(fix)}$), to estimate the variance explained by range, and iii) the difference between the two ($R^2GLMM_{(fix+rand)} - R^2GLMM_{(fix)}$) to estimate the contribution of the random effects only ($R^2GLMM_{(rand)}$) (Nakagawa & Schielzeth, 2013), using the MuMIm package (Barton, 2013). Then, to determine if any difference in species roles between native and exotic range could have occurred due to biogeographical patterns from tropical to temperate zones (Olesen & Jordano, 2002; Schleuning *et al.*, 2012), we re-ran the above models including the absolute latitude as a fixed effect interacting with range. Likewise, we re-ran the models with trophic level (plant or pollinator) and its interaction with range to determine whether any differences between native and alien range only applied to one trophic level.

Does a species' role in the native range predict its role in the alien range?

To test whether a species' role in the native range can predict its role in the alien range, we fitted five linear regressions relating species' mean normalised degree, closeness, betweenness, and the *c*- and *z*-scores in the alien range to the mean values in their native range. Normalised degree was strongly influenced by an outlier, which was removed and consequently improved model fit (Appendix S1). Model validation to check for homoscedasticity and normality of the residuals was performed following Crawley (2013) and Zuur et al. (2009). As previously, we re-ran these regressions including, separately, absolute latitude and trophic level and their interactions with species' role in the native range to determine whether the predictive power depended on these variables. Latitude was determined for each species as the absolute difference between latitudinal mean in the native range and the latitudinal mean in the alien range. The latitudinal mean was obtained by

averaging the absolute latitude of all occurrences each species has in its native and alien ranges.

Subsequently, we jack-knifed the linear regression models to provide an unbiased assessment of how accurately species roles could be predicted in alien networks based on their mean role in the native networks (Efron, 1983). Each species was removed from the linear regression in turn, the regression re-fitted, and predictions of the role metrics were generated for that species in the alien networks based on its mean value across its native networks. The observed mean values in the alien range were then compared against the predicted values using Pearson`s correlations. Individual species roles and mean species roles were tested for correlation (presented as the Spearman coefficient in Table S5) and a Bonferroni correction was used in both LMMs and LMs. All statistical and network analyses were run in R v. 2.15.3 and v. 3.1.1 (R Core Team, 2014).

RESULTS

We compiled information on 12 plant species and five pollinator species that occurred in at least one network in a native range and one network in an alien range (Table 1). These 17 species, from 19 different countries, were distributed in all continents except Antarctica (Fig. 1, Table S1); this translates into a large range of different habitats, climatic conditions and species richness. In total, we worked with 167 occurrences of the 17 target species (i.e. one occurrence corresponds to the occurrence of a species in either its native or alien range; note that multiple target species can occur in the same network) (Table S2).

250

251 **Are there differences in species roles in their native and alien range?**

252 There was no significant difference between native and alien ranges in any of the measures
253 of species' role (Table 2). In other words we found no evidence that, for example, species
254 consistently interact in a more generalist way in their exotic vs. native range. Rather, the
255 variance explained by the models was primarily attributable to the random factors
256 ($R^2GLMM_{(rand)}$ was 94%, 40%, and 20% in the closeness, normalised degree and betweenness
257 models respectively), which were the network and the species identity, whilst range, the fixed
258 term, was not statistically significant for any of the metrics tested (Table 2). Similarly, the
259 random structure explained around one third of the variance in the *z*-score (29%) and the *c*-
260 score models (37%). The large variance retained by the random structure suggests that
261 species differ considerably in their network roles and that, unsurprisingly, species roles
262 depend on the local network (e.g., network size constrains the range of possible roles), and
263 this large variance within native or exotic ranges of a species blurred any significant
264 differences between them.

265 Even though network architecture can change across regions (Olesen & Jordano,
266 2002), we found no systematic change in species roles with latitude, neither significant range
267 x latitude interaction (Table S3). However, a significant range x trophic level interaction for
268 closeness (Table S3) revealed that the native range had lower closeness for pollinators but
269 not for plants. This indicates that pollinators may move into a more central role in their alien
270 range by pollinating generalist plants that are also pollinated by many other species and share
271 those pollinators with many other plants. Given that in our analyses there were more plant
272 species than pollinator species, this interaction effect captured the difference between

ranges for pollinators that was otherwise masked by the lack of difference on plant species. Moreover, pollinator species had higher *c*-scores than plant species independently of range, suggesting that the pollinators included in our analyses may be better network connectors (Table S3). In fact, most plant and pollinator species played peripheral roles in our networks (73%) but pollinators were the main connectors (88%), module hubs (75%) and the only network hubs (100%) (Table S4).

Does a species' role in the native range predict its role in the alien range?

Two measures of species roles, closeness and normalised degree, in the alien range could be predicted from the native range data ($F_{1,15}$ = 27.32, p = 0.0001, r^2 = 0.62 and $F_{1,14}$ = 13.56, p = 0.0025, r^2 = 0.46, respectively; Fig. 2). The coefficients for closeness and normalised degree were 0.98 (SE ± 0.187) and 0.71 (SE ± 0.192), respectively, and both had intercepts that did not differ significantly from zero (closeness: t = 0.25, p = 0.809; normalised degree: t = 0.67, p = 0.512), suggesting that a species' role in the native range is associated to that in the alien range. In contrast, the positive trend in the relationship between native and alien range when estimating betweenness (slope = 0.208 SE ± 0.109) and the *z*-score (slope = 0.412 ± 0.204) was marginally non-significant ($F_{1,15}$ = 3.63, p = 0.076, r^2 = 0.14 and $F_{1,15}$ = 4.07, p = 0.062, r^2 = 0.16, respectively; Fig. 2) and lacked any significance for the *c*-score model ($F_{1,15}$ = 0.22, p = 0.649). Although the testing of correlated variables (Table S5) increases the probability of type I error, the effects for closeness and normalised degree remained significant when a Bonferroni correction was applied (corrected alpha = 0.01). Moreover, out of five variables tested, the probability of finding two significant at an alpha below 0.0025 is extremely low (6.2×10^{-5}, calculated using the Bernoulli process described in Moran 2003), indicating that

overall the suite of species roles in the exotic range could be predicted better from roles in the native range than would be expected by chance.

The predictive effects of closeness and normalised degree were consistent when latitude and trophic level were included in the models (Table S4). Neither latitude (normalised degree: $F_{3,13} = 0.355$, $p = 0.787$; closeness: $F_{3,13} = 1.61$, $p = 0.235$; betweenness: $F_{3,13} = 0.938$, $p = 0.450$; *c*-score: $F_{3,14} = 2.00$, $p = 0.173$; *z*-score: $F_{3,14} = 0.56$, $p = 0.652$) or trophic level (normalised degree: $F_{3,13} = 0.262$, $p = 0.851$; closeness: $F_{3,13} = 1.708$, $p = 0.214$; betweenness: $F_{3,13} = 1.044$, $p = 0.406$; *c*-score: $F_{3,14} = 2.00$, $p = 0.173$; *z*-score: $F_{3,14} = 0.56$, $p = 0.652$) showed any significant interaction with range when tested for predictive effects of species roles from the native to the alien range of a species distribution (Table S4). Congruent with the LMM results, after model selection we detected that the mean *c*-score was also higher for pollinators than for plants independently of range ($F_{2,14} = 12.02$, $p = 0.0009$).

In the jack-knife validation of our predictions, predicted values of closeness in the alien range were highly correlated with the corresponding observed values ($t = 15.339$, $p < 0.0001$, $r = 0.777$), suggesting that the species closeness in the native range is a good predictor of the species closeness in the alien range. The predictive power of native range was lower but still a good predictor for more than half of the species when estimating normalised degree ($t = 9.040$, $p < 0.0001$, $r = 0.583$), *z*-score ($t = 8.0445$ $p = < 0.0001$, $r= 0.53$), and *c*-score ($t = 8.587$, $p < 0.001$, $r = 0.56$), though not as good for betweenness ($t = 5.621$, $p < 0.0001$, $r = 0.401$).

DISCUSSION

Two consistent patterns emerged from our analyses of the 48 datasets: 1) although species differed considerably in their roles, the roles of species generally did not differ consistently between their alien and native ranges, and 2) two metrics of species roles, closeness and normalised degree, in the alien range could be predicted from the native range. Betweenness and *z*-score predictions from the native to the alien range were marginally non-significant, but showed a trend toward positive correlation, which was unsurprising in the case of betweenness, given its high correlation with normalised degree and closeness (Table S5b). Despite this overall predictive ability, we found that pollinators (but not plants) had a higher closeness in their alien range, probably due to their ability to exploit a wide range of resources and thus interact with generalist plants. Still, trophic level (pollinator vs. plants) did not interact significantly with range, except for *c*-score, which showed higher values for pollinators, suggesting they may play a better role in connecting the whole networks than did plants. Our results suggest that species role conservatism may occur, such that species that are generalists or play a central role in their native network are likely to play a similar role in their alien range.

Limitations

In an ideal situation, the networks studied would have been collected using the same methods, aiming for quantitative data collected over similar periods of time. The dataset used comes from different sources that used different sampling methodologies, spatial and temporal scales. Moreover, it contains only species that successfully established in the alien range thus it lacks information for those species that failed to establish in the alien range. Moreover, our models do not consider species abundance, which is known to drive some

network patterns (Blüthgen *et al.*, 2007; Dorado *et al.*, 2011; Staniczenko *et al.*, 2013; Fort *et al.*, 2016) as well as the effects of invasive species (Dostal *et al.*, 2013; Carvalheiro *et al.*, 2014; Traveset & Richardson, 2014). Furthermore, the conservation status of the areas from which the networks were sampled is mostly unknown. Thus, the native range should not be necessarily interpreted as a pristine environment given that we are likely working with altered environments in both ranges. This high heterogeneity in the dataset generated high variance across different networks (even within a species' native or alien range), which would have reduced the probability of detecting differences across 'treatments'. In that sense, the absence of evidence for differences in species roles in native vs. alien range cannot be viewed as evidence of absence. That said, the positive correlations we observed between native- and alien-range values of closeness and normalised degree were robust enough to be seen despite the data being averaged across these heterogeneous replicate networks and spanning species with a range of roles from specialists to generalists.

The intrinsic roles of alien species in pollination networks

The correlation between species roles in their native and alien range in the five network statistics concurs with other authors who report that species have intrinsic properties in ecological networks that persist over temporal and spatial scales (Jordano *et al.*, 2003; Gómez *et al.*, 2010; Stouffer *et al.*, 2012; Baker *et al.*, 2015). From the roles estimated here, high degree and high closeness define the core of the nested network (i.e. those generalists that interact with both specialists and generalists), and our results suggest that core species will tend to maintain this role even when they enter novel communities. Species with high degree, i.e. generalists, are expected to be good invaders because they can increase their chance to

364 establish and spread through the population by interacting with many of the “available”
365 species. Conversely, specialist species with few interactions in the native range will also have
366 only few interactions in the alien range, and this may lower their chance of establishing into
367 the novel community if, for example, the resource is scarce and competition strong (Aizen *et*
368 *al.*, 2008; Aizen *et al.*, 2012), as shown in previous work that simulated invasion of food webs
369 (Romanuk *et al.*, 2009). In turn, high closeness can be seen in species that interact with other
370 central species in the community, even if the focal species is not a generalist itself. In fact, in
371 our dataset the average normalised degree and average closeness were not significantly
372 correlated (r = 0.24, Table S5b), such that a species could occupy a consistently central
373 position in networks by interacting with central species, rather than by being a generalist
374 itself. Therefore, the combination of degree and closeness can potentially be good indicators
375 of species with high risk of introduction success in terms of invasion. On the other hand, the
376 poor prediction of betweenness and the *c*- and *z*-score, which indicate the role a species plays
377 as connecting different parts of the network, suggests that the role of species as connectors
378 may depend on the distribution of species into modules.

379 Most plant species depend on animal species for pollination (Waser & Ollerton, 2006;
380 Ollerton *et al.*, 2011), thereby any characteristic that enhances interactions with pollinators
381 would likely be favourable when colonizing a new area. Central alien plants may have an
382 advantage in the new range in terms of gene flow if local pollinators show high fidelity. A
383 greater number of pollinator species constantly visiting different conspecific flowers may
384 promote greater deposition of conspecific pollen grains, therefore increasing pollination
385 (Brosi & Briggs 2013; Huang *et al.,* 2015). Nevertheless, the benefits of this increased visitation
386 frequency may be partly offset by an increase in heterospecfic pollen transport (Fang & Huang

2013) if, instead, the alien plant interacts with a generalist pollinator that visits different plant species therefore increasing heterospecific pollen transfer, potentially reducing seed set (Ashman & Arceo-Gómez, 2013). Still, heterospecific pollen transfer has been shown to be generally low and have none, low or species-specific effect on plant reproduction (Bartomeus *et al.*, 2008; Montgomery & Rathcke, 2012; Fang & Huang, 2013; Emer *et al.*, 2015). Moreover, central pollinator species may have an advantage over less connected species when arriving in an alien community due to their ability to visit different flower species, thereby obtaining different food resources (Traveset et al, 2013). Pollinators were the main connectors in our networks and that was more frequent in their alien range. Given that the main pollinator connectors in our network were social insects (i.e *Apis mellifera* and *Bombus* spp.), which are usually highly abundant in invaded areas (e.g. Aizen *et al*., 2008; Santos *et al*., 2012), and whose foraging individuals reflect the colony needs (Willmer & Finlayson 2014 and references therein), it may be that these species' roles vary according to their population density and foraging behaviour. Yet, central pollinator species may face high competition with the local pollinators with which they share interactions, a constraint that may make it difficult for pollinators to establish in a novel community with low nectar/pollen resources, for example.

Our findings also have implications for network persistence. Rewiring, i.e. the reshuffling of interaction links among species, can enhance network resilience and robustness to disturbance (Staniczenko *et al.*, 2010; Kaiser-Bunbury *et al.*, 2011; Olesen *et al.*, 2011). Given that both plant and pollinator links can be transferred from native generalist to alien generalist species (Aizen *et al.*, 2008), and that the probability of a native pollinator interacting with an alien plant increases with its degree and nestedness contribution (Stouffer *et al.*, 2014), the introduction of a highly generalist alien species may affect not only the local

generalist species but also the more specialized ones that connect to it via interaction rewiring (Aizen *et al.*, 2008). The consequences of this will depend on the centrality of the introduced species in combination with that of the native species, e.g. highly-connected alien species will likely promote local species rewiring, whilst the arrival of a poorly-connected species (i.e. a specialist) may have a mild or even neutral effect on local species interactions. Moreover, a species that remains in its home range in which the community has changed due to local extinctions and alien species invasion will find itself in a novel network of interactions. Given that species roles are conserved, rewiring of interactions will be needed for the local species to fit into the novel community (Gilljam et *al.*, 2015).

Conclusions

In summary, there seems to be an intrinsic component of species roles in plant-pollinator networks that is conserved across species native and alien ranges. Our results suggest that the core network position that a species occupies when introduced in a novel community will resemble how generalist or specialist it is in its native community. Our results provide new insights into the recent literature about interactions and species role conservatism, and have implications regarding the potential links that alien species may be able to create or disrupt once introduced into novel communities. Further studies incorporating community traits and the phylogenetic relationship between species with species network roles will advance our understanding of how alien species interact with, and potentially drive the formation of, novel communities.

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SUPPORTING INFORMATION

Additional Supporting Information can be found in the online version of this article:

APPENDIX S1. Outlier detection analyses.

TABLE S1 – Description of the networks used for the analyses of the species' roles of plants and pollinators in the alien and native range.

TABLE S2. List of the target species and the networks in which they were recorded. Network ID follows Figure 1 and Table S1 in which details of each network are provided.

TABLE S3. Results of the Linear Mixed-Effect Models (LMMs) and the Linear Regression Models (LMs) testing whether latitude and trophic level interact with species range to determine species' roles.

TABLE S4. Species roles on pollination networks following Olesen et al. (2007): Peripheral $z \leq 2.5$, $c \leq 0.62$; Connector $z \leq 2.5$, $c > 0.62$; Module hub $z > 2.5$, $c \leq 0.62$; Network hub $z > 2.5$, $c > 0.62$. The first number is the number of occurrences in networks in the species native range, and the second number is the species occurrences in networks in its alien range.

TABLE S5. Correlation between normalised degree, closeness, betweenness, *c* and *z* scores measured with (a) individual entries, i.e. the value of the role of each species in each network

678 is taking into account, as used in the Linear Mixed Models, and (b) when the averages for each
679 species are considered, as used in the Linear Regressions of the manuscript. Values
680 correspond to the Spearman correlation coefficient ρ.

681

682

683 **BIOSKETCHES**

684 **Carine Emer** is a community ecologist interested on understanding how anthropogenic
685 disturbance affect animal-plant interactions. Her research includes both mutualistic and
686 antagonistic processes in tropical and temperate habitats. Recently she has studied the
687 effects of invasive species, habitat loss and fragmentation on ecological networks. She is
688 currently a postdoctoral researcher at the Universidade Estadual Paulista (UNESP) in Brazil.
689 The authors are part of a collaboration established during her doctorate at the University of
690 Bristol, UK.

691 **Authors contributions:** CE and JMT developed the study framework. CE gathered the data,
692 ran the analyses, and wrote the manuscript. IPV provided statistical advice. DM contributed
693 with the study design and discussion. JM advised on the collection of the field data, and JM
694 and JMT commented and edited the versions of the manuscript.

695

696 **TABLES AND FIGURES LEGEND**

697

698 **Table 1**. The 17 plant and pollinator species analysed in this study (see Table S1 for further
699 information about each network).

700 **Table 2.** Results of the Linear Mixed-Effects Models (LMMs) testing whether species roles
701 differ from the native to the alien range. Pseudo R-squared values were calculated to estimate
702 the variance explained by the fixed and random structure of each model: $R^2_{fix+rand}$ - estimates
703 total variance explained by the fixed and random effects combined; R^2_{fix} - estimates the
704 variance explained by range; R^2_{rand} estimates the contribution of the random effects only.

705 **Figure 1.** The location of the 48 plant-pollinator networks. Panels A-G show the location of
706 those networks that overlap in the full map. Numbers are the individual codes of each
707 network identity (see Supplementary Material).

708 **Figure 2**. Results of the linear regression models testing whether a species' role in the native
709 range predicts its role in the alien range. (a) Normalised degree; (b) Closeness; (c)
710 Betweenness; (d) *c*-score; and (e) *z*-score. Results of normalised degree are shown after the
711 removal of an outlier.

712 **Table 1**

		Number of networks present	
Plant species	**Family**	**Native networks**	**Alien networks**
Achillea millefolium L.	Asteraceae	4	5
Cirsium arvense (L.) Scop	Asteraceae	3	6
Cytisus scoparius (L.) Link	Fabaceae	1	1
Eupatorium cannabinum L.	Asteraceae	1	2
Hieracium pillosela L.	Asteraceae	2	4
Hypochaeris radicata L.	Asteraceae	5	6
Leucanthemum vulgare Lam.	Asteraceae	2	4
Lotus corniculatus L.	Fabaceae	3	1
Taraxacum officinale F.H. Wigg	Asteraceae	4	1
Trifolium pratense L.	Fabaceae	2	4
Trifolium repens L.	Fabaceae	3	10
Verbascum thapsus L.	Scrophulariaceae	2	3
Total plants` occurrences		31	47
Insect species	**Order**		
Apis mellifera L.	Hymenoptera	9	28
Bombus hortorum L.	Hymenoptera	7	4
Bombus terrestris L.	Hymenoptera	9	6
Eristalis tenax L.	Diptera	5	11
Pieris rapae L.	Lepidoptera	3	6
Total insects` occurrences		33	46
Total		64	102

713

714 **Table 2**

	Linear Mixed-Effects Models					
	Est	t	p	$R^2_{fix\text{-}rand}$	R^2_{fix}	R^2_{rand}
Normalised degree	0.305	1.227	0.226	0.408	0.011	0.397
Closeness	-0.108	-1.188	0.237	0.939	0.003	0.936
Betweenness	0.116	0.326	0.747	0.201	0.000	0.201
***z* – score**	-0.029	-0.158	0.875	0.285	0.000	0.285
***c* - score**	0.028	1.076	0.285	0.378	0.010	0.377

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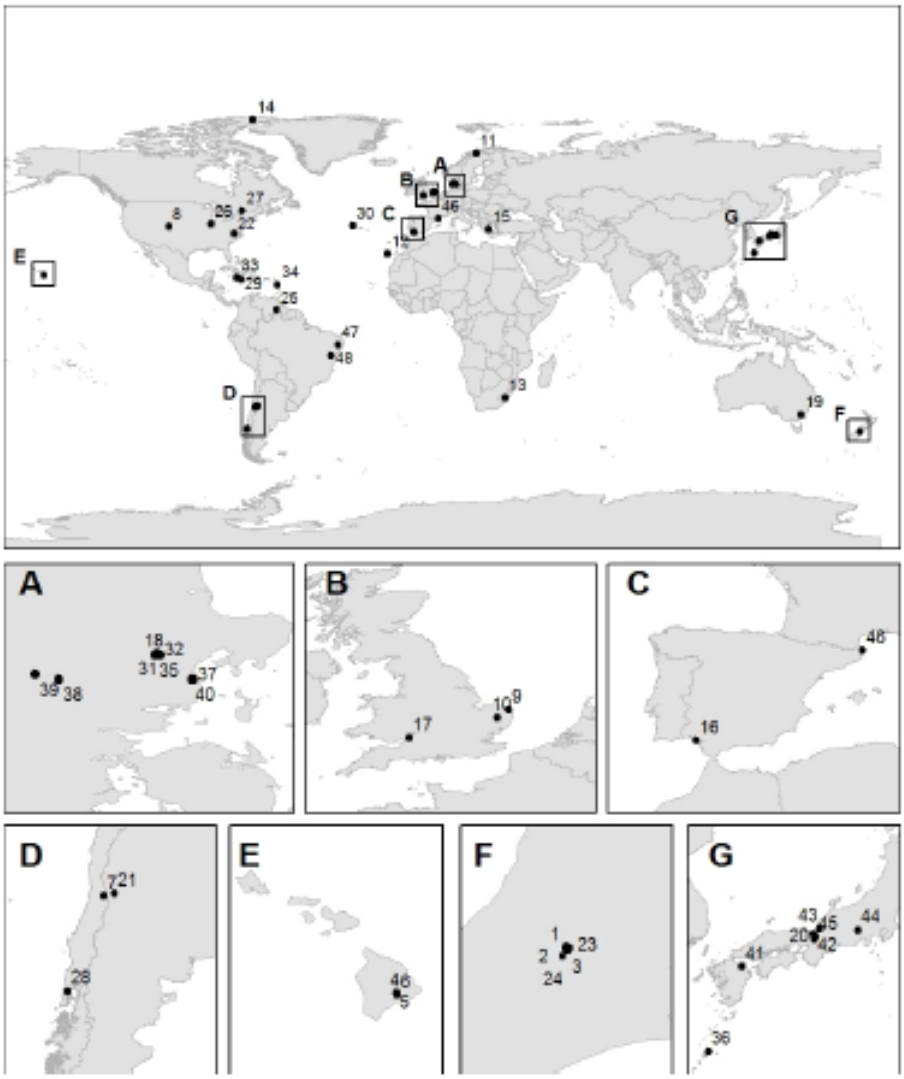

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720 **Figure 1**

721

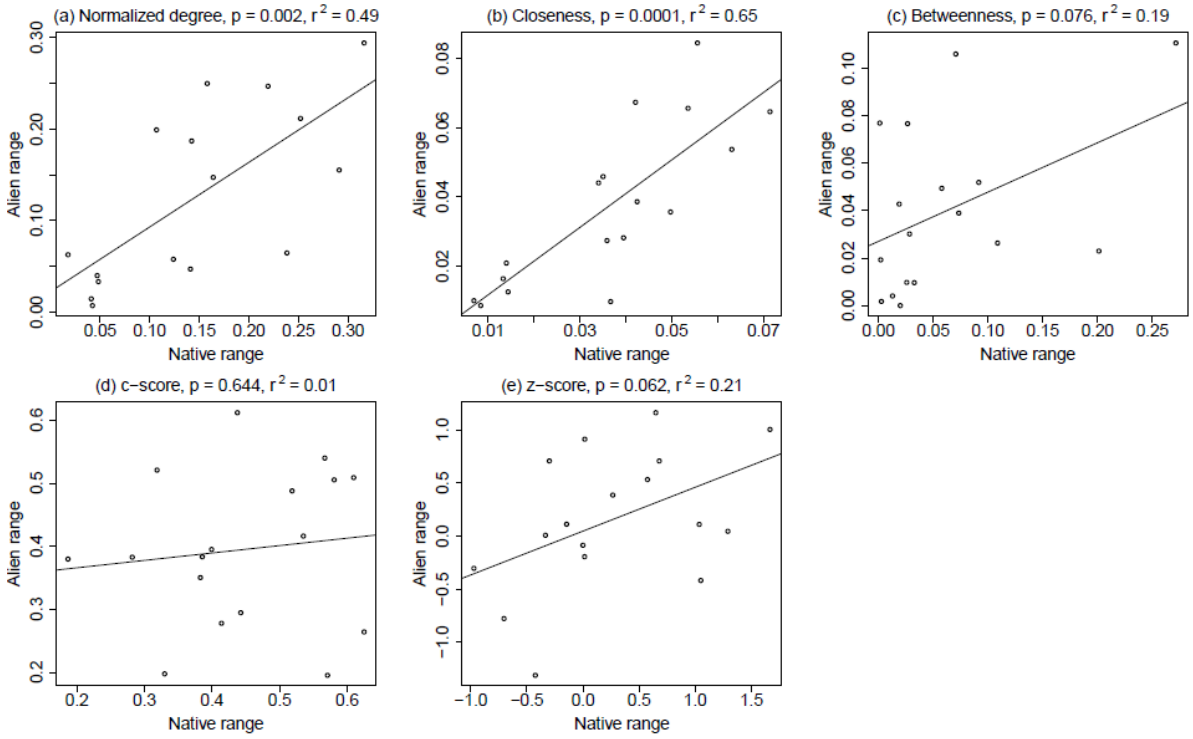
(a) Normalized degree, p = 0.002, r2 = 0.49
(b) Closeness, p = 0.0001, r2 = 0.65
(c) Betweenness, p = 0.076, r2 = 0.19
(d) c−score, p = 0.644, r2 = 0.01
(e) z−score, p = 0.062, r2 = 0.21
Alien range
Native range

Figure 2